

Body Size and Reproductive Tactics in Varanid lizards

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Abstract Body size and female reproduction in the water monitor lizard (*Varanus salvator*) were studied. Forty-two adult females larger than 500 mm SVL and 32 adult males larger than 400 mm SVL were donated by local people in Ledong, Hainan under permit to our laboratory in Hainan in 2013 and 2014. The largest male and female measured 745 and 755 mm SVL, respectively. The mean SVL was greater in adult females than in adult males. Males had larger heads (head width) than females of the same SVL. The smallest reproductive female in our sample was 565 mm SVL. Females produced a single clutch of 17.1 (10–23) pliable-shelled eggs per breeding season stretching from mid-June and mid-September. Clutch size and clutch mass were all positively related to female SVL. However, there was no significant linear relationship between egg mass and female SVL. Larger females generally produced more eggs, and thus heavier clutches than did smaller ones. There was no significant linear relationship between relative clutch mass and female SVL. Phylogenetic generalized least squares (PGLS) analysis, accounting for phylogenetic relationships, showed that clutch size was positively correlated with mean maternal SVL in varanid lizards. PGLS analysis showed that phylogenetic relationships did not affect clutch (or/and egg) mass and the SVL although there were significant linear relationship between clutch (or/and egg) mass and mean maternal SVL. Therefore, we could draw some general conclusions about the body size and reproductive tactics in varanid lizards that larger females generally produced more eggs, larger eggs and thus heavier clutches than did smaller ones.

Keywords body size, female reproduction, monitor lizard, Varanidae

1. Introduction

Fifty-three species of *Varanus* are now currently recognized worldwide (Pianka and King, 2004). They are morphologically conservative but vary widely in size (Pianka, 1994). Such a diverse monophyletic group can be exploited both to identify and to understand the actual course of evolution. Small body size has evolved three times among varanids, in the Australian *Odatia*

clade, and, in the Asian clade, in *V. flavescens* and in the *prasinus* species complex; large body size also evolved in *V. bengalensis* and *V. salvator* in the Asian clade and independently in the common ancestor to *V. salvadorii*, *V. komodoensis*, and *V. varius*, as well as in the Australian perentie *V. giganteus* (Pianka, 1994).

Thopson and Pianka (2001) reviewed various aspects of the evolution of reproductive tactics among monitor lizards. Body size influences reproductive tactics more strongly than phylogeny; eggs of small species are laid in the spring and hatch in the summer; eggs of larger species are laid later, often overwinter, and the next year; smaller species have relatively larger hatchlings and larger clutch size compared with adult size than do larger

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Received: 26 October 2014 Accepted: 9 December 2014

species. However, most of the conclusions are drawn by accounting for the maximum snout-vent length (SVL) rather than average maternal SVL, which is a better variable. Moreover, these data were collected more than ten years ago and new data are available. It is necessary to take a new review on these aspects.

Among the fifty-three species of *Varanus*, the water monitor lizard (*V. salvator*) is a relatively large-sized lizard. It has the largest distribution area of all recent varanids. It is recorded from Bangladesh, Brunei, Burma, southwestern China, northeastern India, Indonesia, Kampuchea, Laos, Malaysia, Singapore, Sri Lanka, Thailand, and Vietnam (Smith, 1932; Pianka and King, 2004). It has a wide range of variation in body size from hatchling to adulthood, and this feature makes the lizard well suited to the studies addressing the role of body size in influencing reproductive strategy. Here, we studied sexual dimorphism and female reproduction in *V. salvator* at the our laboratory in Hainan, China between 2013 and 2014 to evaluate sexual dimorphism in morphological characters such as body size and head size, and to investigate the relationships among clutch size, egg mass, clutch mass and female size in *V. salvator*. We also collected data from recently published references in female reproductive characteristics in varanid lizards, using the maternal SVL instead of maximum SVL, to examine different reproductive variables relationships while accounting for phylogenetic relationships.

2. Materials and methods

Forty-two adult females larger than 500 mm SVL and 32 adult males larger than 400 mm SVL were donated by local people in Ledong, Hainan under permit to our laboratory in Hainan in 2013 and 2014. All lizards were maintained in 30 m × 30 m × 2 m (length × width × height) enclosures, of which each was half-covered by a sun-shading net, had a 5 m × 5 m × 0.4 m pond, tree branches and bark hides, and housed 12–14 individuals. Chicken (*Gallus gallus domestica*) and fish (*Tilapia mossambica*) were provided daily so that excess food was always available. All enclosures were serviced weekly. This included cleaning or changing water in the pond, removing fecal matter, slough and dead food items, and checking animal well-being. The lizards were disturbed only if measuring, weighing or physical examinations were required.

Morphological measurements taken for each individual included body mass, snout-vent length (SVL), abdomen length (the distance between the points of insertion of

the fore- and hind-limbs), tail length, forelimb length (humerus plus ulna), hindlimb length (femur plus tibia), head length, head width, interorbital distance, nostril diameter, internasal distance, 4th finger length, 4th toe length, eye diameter and tympanum diameter. All of these measurements were taken when the lizards calmed down, without anesthetics.

Egg-laying activities were monitored in real time using an infrared video camera with 16 probes, such that eggs could be always collected, measured and weighed soon after being laid. SVL and body mass were taken for each postpartum female. Eggs were measured for length and width and weighed. Relative clutch mass was calculated by dividing clutch mass by the female postpartum mass.

Prior to parametric analyses, all data were tested for normality using the Kolmogorov-Smirnov test and for homogeneity of variances using the Bartlett's test. We used one-way analysis of variance (ANOVA) and one-way analysis of covariance (ANCOVA) to analyze the corresponding data. The homogeneity of slopes was checked prior to testing for differences in the adjusted means. Throughout this paper, values are presented as mean ± SE, and the significance level is set at $\alpha = 0.05$. Ordinary least squares (OLS) regression estimation was used to estimate slope for all conventional analyses. OLS regression was implemented on the R 2.15.3 (R Development Core Team, 2013), using the SMATR packages (Warton *et al.*, 2012). We used phylogenetic generalized least squares (PGLS) regression methods (Martins and Hansen, 1997; Garland and Ives, 2000; Rohlf, 2001) to examine different variables relationships (e.g. SVL and clutch size / clutch mass / egg mass) while accounting for phylogenetic relationships among species. PGLS which is functionally equivalent to phylogenetically independent contrast method (Felsenstein, 1985; Garland and Ives, 2000) when assuming that residual variation between species is correlated through an evolutionary process along the specified phylogenetic tree similar to a Brownian-motion model. PGLS incorporates phylogenetic information into generalized linear models offers a powerful method for analyzing continuous data that has been applied to estimation the evolutionary model and the relationships among life-history traits (Warne and Charnov, 2008; Barros *et al.*, 2011). The PGLS method fits a linear model according to phylogenetic non-independence between data points. The strength and type of the phylogenetic signal in the data matrix can also be elucidated by adjusting branch length transformations, which can be optimized to find the maximum likelihood transformation

given the data and the models (Orme *et al.*, 2012). We used λ to analysis phylogenetic effects ($\lambda = 0$ indicates no phylogenetic effect, and $\lambda = 1$ indicates a strong phylogenetic effect equivalent to that expected under the Brownian motion model) and Akaike Information Criterion (AIC) to estimate merits and drawbacks of the models in the set used and the best model has the lowest AIC. PGLS regression analysis was implemented with the R package caper (Orme *et al.*, 2012). The tests detailed previously were carried out using the topology including all collected species. This topology of species was based on proximate phylogenetic correlation assembled from Pyron *et al.* (2013). This tree were drawn using Mesquite (Maddison and Maddison, 2011). Because branch lengths were lacking divergence time, genetic distance or any other metric proportional to the expected variance for the evolution of each analyzed trait are unavailable, we arbitrarily set initial branch length to a value of 1, which is appropriate for a speciation model of evolution (Martins and Garland, 1991).

The model with better fit can be determined by a maximum-likelihood ratio test in which twice the difference in the natural log of the maximum likelihoods (LnL) of the OLS and PGLS models will be distributed approximately as a χ^2 with degrees of freedom equal to the difference in the number of parameters estimated in the two models (Warne and Charnov, 2008).

3. Results

Sexual dimorphism All the other 13 morphometric variables were positively correlated with SVL (each $P < 0.05$). The largest male and female measured 745 and 755 mm SVL, respectively. The mean SVL was greater in adult females (641.0 ± 9.4 mm, $N = 42$) than in adult males (601.0 ± 13.5 mm, $N = 32$; ANOVA, $F_{1,72} = 6.314$, $P = 0.014$); males had larger heads (HW) than females of the same SVL, whereas between-sex differences in the other 12 morphometric variables were not found (Table 1).

Female reproduction The smallest reproductive female in our sample was 565 mm SVL. Females produced a single clutch of 17.1 (10–23) pliable-shelled eggs per breeding season stretching from mid-June and mid-September (Table 2). Clutch size ($r = 0.82$, $F_{1,12} = 24.798$, $P < 0.001$) and clutch mass ($r = 0.68$, $F_{1,12} = 10.451$, $P = 0.007$) were all positively related to female SVL (Figure 1). However, there was no significant linear relationship between egg mass and female SVL ($F_{1,12} = 0.014$, $P > 0.05$). Larger females generally produced more eggs, and

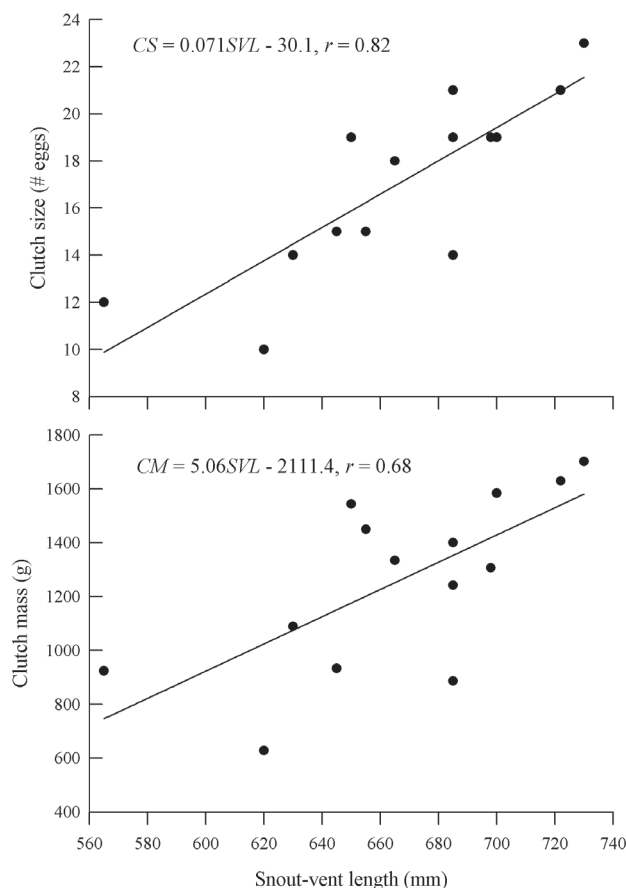


Figure 1 Linear regressions of clutch size and clutch mass on female SVL in *Varanus salvator*. Regression equations and coefficients are given in the figure.

thus heavier clutches than did smaller ones. There was no significant linear relationship between relative clutch mass and female SVL ($F_{1,12} = 0.008$, $P = 0.929$).

Reproductive tactics in Varanid lizards We assembled published and our own research data on mean maternal SVL, clutch size, clutch mass, and egg mass for Varanid lizards (Table 3). Data from 30 species of Varanid lizards show that mean clutch size ranged from 3.4 eggs to 25.5 eggs and the size of gravid females ranged from 91 mm to 1340 mm. Table 4 summarizes the relationships among female reproductive traits in Varanid lizards according to OLS and PGLS analyses. Mean clutch size was positively correlated with mean SVL in both the OLS and PGLS model; and on the basis of likelihood ratio tests, PGLS model were better than OLS model (Figure 2, Table 4). PGLS analysis showed that phylogenetic relationships did not affect clutch (or/and egg) mass and the SVL (both $\lambda = 0$) although there were significant linear relationship between clutch (or/and egg) mass and mean maternal SVL (Figure 2, Table 4).

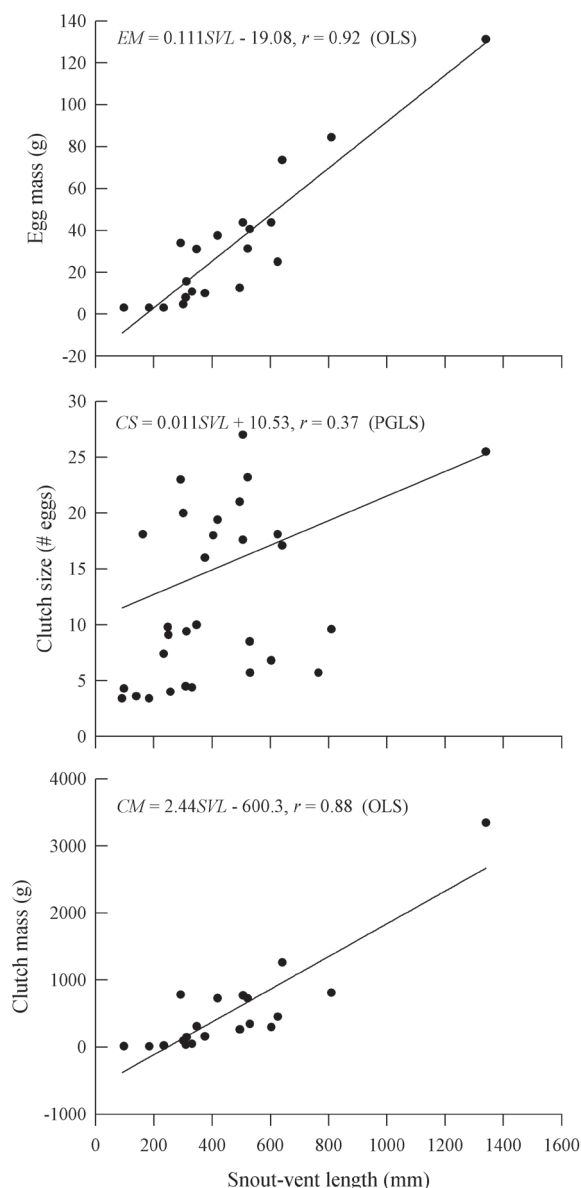


Figure 2 Ordinary least squares (OLS) regression of egg mass and clutch mass on female SVL, and phylogenetic generalized least squares (PGLS) regression of clutch size on female SVL in varanid lizards. Regression equations and coefficients are given in the figure.

4. Discussion

External morphological characters are conventionally used to describe monitor lizard species and are categorized into meristic (quantified using numbers or counts) and morphometric (quantified by measurements) features (Arida and Böhme, 2010). Among the 14 morphometric variables measured, only SVL and HW showed between-sex differences. Males had larger heads (HW) than females of the same SVL, whereas females had larger SVL than males. Male water monitor lizards

have larger heads than females, suggesting that sexual selection could have been a factor in the evolution of large heads of varanid lizards. Larger heads (hence large mouth) have an edge in the process of combat. Male-male ritual combat is pronounced in *V. salvator*, with males standing erect on their hind legs and tail, chests pressed together, grappling with their forelegs wrapped around each other (Pianka and King, 2004). The two contenders try to throw one another off balance during the “clinch phase”; sometimes the winner bites the loser (King and Green, 1999). Females having larger SVL is related to female reproduction. Females should be the larger sex in species where reproductive success is more tightly linked to body size in adult females. Selection acting to increase fecundity and litter volume is the main cause for increased female size in *Gekko japonicus* (Japanese gecko; Ji *et al.*, 1991), *Sphenomorphus indicus* (brown forest skink; Ji and Du, 2000), and *Phrynocephalus vlangalii* (Qinghai toad-headed lizard; Zhang *et al.*, 2005). Previous studies (Mertens, 1942; Shine *et al.*, 1996) reported that tail length shows ontogenetic and sexual dimorphism (short in older ones and longer in males) in *V. salvator*, but we did not find between-sex differences in tail length in this study.

Previous studies reported that *V. salvator* eggs are very variable in size, a length of 64 to 82.6 mm, a width of 32.3 to 45 mm, and a weight of 30 to 87.2 g is reported from different countries, with a high size variability occurring in one population and even in different clutches of one female (Schmidt, 1927; Meer Mohr, 1930; Kratzer, 1973; Anonymous, 1978; Vogel, 1979; Biswas and Kar, 1981; Moharana and Pati, 1983; Andrews and Gaulke, 1990). In this study, egg length, egg width and egg mass also show large variation (Table 2), however, none of them was significantly related to female SVL. Maybe egg size is more associated with other factors such as food availability, water and even heat.

Our results indicated no significant linear relationship between relative clutch mass and female SVL. In a previous study, relative clutch mass of *V. tristis* (with large clutch size of 10 eggs) is similar to that of other sympatric desert varanids with smaller clutch size (Pianka, 1994), suggesting that its larger clutch is achieved at the expense of relative neonate size (hatchling *V. tristis* are relatively small compared to adults). Thus, it seems that relative clutch mass remains relatively constant not only within but also between species.

Pianka and King (2004) reported that clutch size in *V. salvator* ranged from 5 to 22 eggs, with a mean of 13 eggs (data collected during different visits to a skinnery in

Table 1 Descriptive statistics, expressed as mean \pm SE and range, for size and morphology of 74 water monitor lizards (42 females, and 32 male). Results of one-way ANOVA (for SVL and variables with a mark of †) or ANCOVA (for the remaining variables) with SVL as the covariate are given in the table. Variables with a mark of † were analyzed using unequal slopes models.

	Females	Males	Results of ANOVA or ANCOVA
Snout-vent length (mm)	641.0 \pm 9.4 515–755	601.0 \pm 13.5 405–745	$F_{1,72} = 6.31, P = 0.014$ Females > Males
Body mass (kg)	5.5 \pm 0.3 2.7–9.2	4.5 \pm 0.4 1.3–9.7	$F_{1,71} = 0.13, P = 0.909$
Abdomen length (mm)	379.7 \pm 6.1 300–470	354.6 \pm 9.0 244–432	$F_{1,71} = 0.01, P = 0.911$
Tail length (mm)	955.7 \pm 18.0 630–1115	918.8 \pm 20.6 612–1146	$F_{1,71} = 0.67, P = 0.417$
†Head length (mm)	109.8 \pm 1.2 90.4–125.2	106.3 \pm 2.0 78.2–132.6	$F_{1,72} = 3.35, P = 0.071$
†Head width (mm)	51.4 \pm 0.7 42.1–59.6	49.7 \pm 1.3 35.0–69.7	$F_{1,72} = 6.47, P = 0.013$ Females < Males
Nostril diameter (mm)	7.2 \pm 0.2 4.3–9.0	6.7 \pm 0.2 3.8–9.7	$F_{1,71} = 0.02, P = 0.885$
†Eye diameter (mm)	20.9 \pm 0.2 17.8–23.3	20.4 \pm 0.4 16.6–25.0	$F_{1,72} = 0.16, P = 0.689$
Tympanum diameter (mm)	10.8 \pm 0.2 8.0–13.2	10.8 \pm 0.3 7.6–14.7	$F_{1,71} = 2.46, P = 0.121$
†Internasal distance (mm)	15.9 \pm 0.2 13.6–18.5	15.3 \pm 0.4 10.7–19.3	$F_{1,72} = 0.27, P = 0.606$
†Interorbital distance (mm)	33.0 \pm 0.4 27.8–37.9	31.5 \pm 0.7 23.2–38.7	$F_{1,72} = 0.002, P = 0.968$
Forelimb length (mm)	150.7 \pm 1.8 124–173	141.8 \pm 3.1 95–168	$F_{1,71} = 0.50, P = 0.491$
Hindlimb length (mm)	186.5 \pm 2.9 146–223	177.4 \pm 4.0 122–225	$F_{1,71} = 1.65, P = 0.203$
4th finger length (mm)	42.4 \pm 0.8 31.1–52.2	40.5 \pm 0.9 27.3–50.3	$F_{1,71} = 0.54, P = 0.466$
4th toe length (mm)	57.8 \pm 0.7 49.0–66.6	57.4 \pm 1.1 44.5–69.9	$F_{1,71} = 3.59, P = 0.062$

Table 2 Descriptive statistics, expressed as mean \pm SE and range, for female reproductive characteristics of *Varanus salvator*.

<i>n</i> = 14	Mean	SE	Range
Snout-vent length (mm)	666.8	11.7	565–730
Post-oviposition body mass (kg)	5.8	0.31	3.59–8.58
Clutch size	17.1	1	10–23
Clutch mass (g)	1260.8	86.7	627.8–1701.6
Egg mass (g)	73.6	2.6	62.2–96.7
Egg length (mm)	74.9	1.3	67.2–82.7
Egg width (mm)	42.3	0.5	39.8–46.3
CV of egg mass (%)	6.5	1	3.0–16.8
CV of egg length (%)	4.1	0.5	2.1–9.6
CV of egg width (%)	3	0.3	1.6–5.7
Relative clutch mass	0.22	0.01	0.11–0.30

South Sumatra). In a breeding group of *V. salvator* at the Madras Crocodile Bank, India (originating from Orissa, India), females laid one or two clutches per year, with a mean clutch size of 13.8 (Andrews and Gaulke, 1990). All mature males investigated in skinneries in North Sumatra were reproductively active, with clutch size ranging from 6 to 17 eggs (Shine *et al.*, 1998). In this study, female

monitor lizards produced a single clutch of 17.1 (10–23) pliable-shelled eggs per breeding season. Eggs were eaten by other neighbor monitor lizard during ovipositions. We observed the phenomenon of cannibalism by an infrared video camera installed in the enclosure. Thus, smaller clutch size reported in previous studies might be caused by the neglect of this cannibal behavior.

Table 3 Descriptive statistics for female reproductive characteristics in varanid lizards. Data were collected from 6 references (Pianka, 1995; Thompson and Pianka, 2001; Pianka *et al.*, 2004; Gaikhorst *et al.*, 2010; Xu *et al.*, 2010; Mendyk, 2011).

Species	SVL (mm)	Clutch size	Egg mass (g)	Clutch mass (g)
<i>V. acanthurus</i>	250	9.1		
<i>V. albigularis</i>	506	27		
<i>V. beccari</i>	309	4.5	8	36
<i>V. bengalensis</i>	495	21	12.5	262.5
<i>V. breviceuda</i>	91	3.4		
<i>V. caudolineatus</i>	97	4.3	3.125	13.4375
<i>V. dumerilii</i>	292	23	34	782
<i>V. eremius</i>	140	3.6		
<i>V. exanthematicus</i>	404	18		
<i>V. flavescens</i>	375	16	10	160
<i>V. giganteus</i>	809	9.6	84.375	810
<i>V. gilleni</i>	184	3.4	3.125	10.625
<i>V. gouldii</i>	312	9.4	15.625	146.875
<i>V. griseus</i>	625	18.1	25	452.5
<i>V. indicus</i>	530	5.7		
<i>V. komodoensis</i>	1340	25.5	131.25	3346.875
<i>V. melinus</i>	347	10	31	310
<i>V. mertensi</i>	529	8.5	40.625	345.3125
<i>V. mitchelli</i>	301	20	4.77	95.4
<i>V. niloticus</i>	522	23.2	31.25	725
<i>V. olivaceus</i>	506	17.6	43.75	770
<i>V. panoptes</i>	603	6.8	43.75	297.5
<i>V. prasinus</i>	331	4.4	10.8	47.52
<i>V. scalaris</i>	257	4		
<i>V. spenceri</i>	419	19.4	37.5	727.5
<i>V. storri</i>	162	18.1		
<i>V. timorensis</i>	234	7.4	3.125	23.125
<i>V. tristis</i>	248	9.8		
<i>V. varius</i>	765	5.7		

Table 4 Regressions of clutch size (CS), clutch mass (CM) and egg mass (EM) on snout-vent length (SVL) in varanid lizards based on ordinary least squares (OLS) regression and phylogenetic generalized least squares (PGLS) regression. ^a On the basis of likelihood ratio tests, the models which are labeled statistically significantly are better than the corresponding regression models between same variables. Significant associations between variables are shown in bold.

Models	Variables	<i>n</i>	Slope	Elevation	<i>r</i> ²	ln likelihood	AIC	λ	<i>F</i>	<i>P</i>
OLS	CS	30	0.013 ± 0.005	7.203 ± 2.480	0.178	−99.789	205.577		<i>F</i> _{1,28} = 6.101	0.02
	CM	20	2.441 ± 0.314	−600.255 ± 167.437	0.770	−145.572	297.143		<i>F</i> _{1,18} = 60.373	<0.0001
	EM	20	0.111 ± 0.011	−19.080 ± 5.962	0.845	−78.867	163.735		<i>F</i> _{1,18} = 98.406	<0.0001
PGLS	CS	30	0.011 ± 0.005	10.534 ± 4.334	0.138	−95.972 ^a	199.943	0.61	<i>F</i> _{2,28} = 4.473	0.043
	CM	20	2.478 ± 0.337	−622.852 ± 183.671	0.750	−144.056	296.112	0	<i>F</i> _{2,18} = 50.023	<0.0001
	EM	20	0.109 ± 0.013	−18.645 ± 7.163	0.793	−79.171	166.341	0	<i>F</i> _{2,18} = 69.056	<0.0001

There are two basic consensuses on clutch size: (1) Clutch sizes are larger and more variable among larger species [e.g., *V. spenceri* has much larger clutch size (20 eggs) than does its similar-sized sister species, *V. mertensi*, which lays only about 8 eggs; *V. salvator* are considerably larger than their sister species, *V. rudicollis*, and the former species lay 17 eggs (in this study, Table 2), where as the latter lays 8 eggs]; (2) Maternal SVL influences clutch size much more strongly within a species than it does between species (Purvis and Rambaut,

1995; Thompson and Pianka, 1999, 2001; Pianka and King, 2004). In this study, clutch size and clutch mass were all positively related to female SVL (Figure 1). Larger females generally produced more eggs, and thus heavier clutches than did smaller ones in *V. salvator*.

PGLS analysis, accounting for phylogenetic relationships, showed that clutch size was positively correlated with mean maternal SVL (Figure 2, Table 4). PGLS analysis showed that phylogenetic relationships did not affect clutch (or/and egg) mass and the SVL

although there were significant linear relationship between clutch (or/and egg) mass and mean maternal SVL (Figure 2, Table 4). Similar results were found in some *Phrynocephalus* lizards, which indicated that ecological processes play a more important role than phylogeny in shaping patterns of reproductive variation (Jin *et al.*, 2003). Therefore, we could draw some general conclusions about the body size and reproductive tactics in varanid lizards that larger females generally produced more eggs, larger eggs and thus heavier clutches than did smaller ones.

Acknowledgements Financial supports were provided by grants from Natural Science Foundation of China (31270571) and Hainan Key Program of Science and Technology (ZDXM20110008) and 131 Talent Project of Hangzhou City. We are grateful to Yanfu QU for assistance in the laboratory.

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